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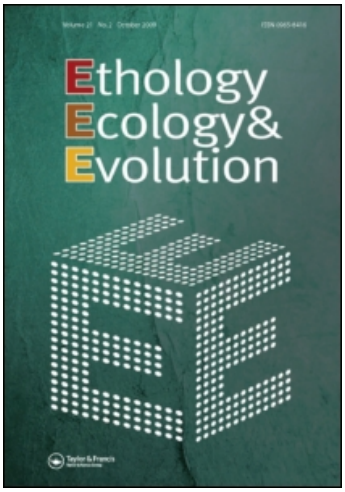

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Changes in ground-foraging ant assemblages along a disturbance gradient in a tropical agricultural landscape

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Changes in ground-foraging ant assemblages occurring along an agricultural intensification gradient were analysed in Nicaragua (Central America). Five habitat types were compared: secondary forest fragments, organic shade coffee and cocoa plantations, corn fields and active pastures. Ants were captured by tuna baiting following standardised protocols. Species richness and diversity decreased along the gradient from forest to the pasture, and each of the agricultural systems (cocoa, coffee and corn plantations) significantly differed in diversity. Species composition also differed along the disturbance gradient, as shown by multivariate analysis. Forest and pasture were at the extremes of the gradient and shared no common species. The ant assemblages associated with coffee plots, although poorer in species, were more similar to those of the forest than to those of the cocoa plantations. The observed trends confirm that shaded agro-forestry plantations can help to maintain high biodiversity levels in tropical landscapes.

KEY WORDS: ant assemblages, agroforestry, biodiversity, managed ecosystems, Nicaragua.

INTRODUCTION

Land conversion to human use (mainly agriculture) is commonly considered a major cause of biodiversity loss, at both global and regional scales (e.g. MATSON et al. 1997; SÁNCHEZ-AZOFEIFA et al. 2001; HELMUTH & LAMBIN 2002). About 35% of the Earth's surface is currently used for agriculture (FOLEY et al. 2007) and a further 10^9 ha of natural ecosystems are expected to be converted to agriculture by 2050 (TILMAN et al. 2001). Indeed, only a small fraction of the global land surface is not directly or indirectly influenced by human activities (KAREIVA et al. 2007). These data generate serious concern for the future of biodiversity conservation but also suggest that the long-established practice of concentrating only on the conservation of pristine or lightly impacted

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habitats is destined to fail (VANDERMEER & PERFECTO 2007; PERFECTO & VANDERMEER 2008). Since human-affected lands cover much of the terrestrial surface, it might be argued that preserving biological diversity in managed ecosystems may allow for the conservation of more species. Furthermore, small patches of pristine habitats may not be suitable for the long-term conservation of species, particularly when they are surrounded by huge expanses of disturbed habitats that restrict species migration and movements (LOVEJOY et al. 1986; BURKEY 1989; BIERREGAARD et al. 1992; VANDERMEER & CARVAJAL 2001). Hence, intervening on the quality of the habitat matrix may be a more fruitful practice for long-term biodiversity conservation (VANDERMEER & PERFECTO 2007; PERFECTO & VANDERMEER 2008).

With this perspective, sound agricultural practices play a crucial role, since a habitat matrix often consists mainly of agricultural land. Some types of managed ecosystems can host a rich and diverse fauna, not much different from that of unmanaged ones (e.g. PIMENTEL et al. 1992; VANDERMEER & PERFECTO 1997; COLLINS & QUALSET 1999; SCHROTH et al. 2004). In a few particular cases, agriculture may also help to enhance biodiversity at the landscape level (TSCHARNTKE et al. 2005 and references therein). In the tropics, permanent crops such as shade coffee or cocoa, which integrate trees into agricultural landscapes, may play an important role in biodiversity conservation. Shade coffee systems have been recognised as potential refuges for forest species (BRASH 1987; PERFECTO et al. 1996, 2003, 2005; GREENBERG et al. 1997; KOMAR 1998; MOGUEL & TOLEDO 1998; PHILPOTT & DIETSCH 2003; PHILPOTT et al. 2006, 2008 and references therein). Similarly, traditional cocoa production has proved to support high levels of biological diversity (RICE & GREENBERG 2000; REITSMA et al. 2001; SCHROTH et al. 2004; WALTERT et al. 2004; HARVEY et al. 2005; KESSLER et al. 2005; MCNEELY & SCHROTH 2006). At the other extreme, large scale monocultural production of 'estate crops', such as banana, pineapple and intensively grown coffee simplify landscapes and reduce floral and faunal diversity (HELMUTH & LAMBIN 2002; TILMAN et al. 2002); hence, they are among the major causes of biodiversity loss in tropical countries (VANDERMEER & PERFECTO 1995). Similarly, corn fields and pastures represent low-diversity poorly structured agro-ecosystems, where little or nothing of the original vegetation is maintained.

Ranking land-use types in terms of their contribution to biodiversity maintenance is thus an imperative goal for conservation biology. The relationship between management intensity and biodiversity has elicited significant debate and, although there is general consensus about the extremes (e.g. forest vs monoculture), there is still controversy over the intermediate steps (VANDERMEER et al. 1998). For this reason, comparative studies of the effects of different land-use strategies on biodiversity (e.g. WILSON & JOHNS 1982; JOHNS 1985; ANDOW 1991; ROTH et al. 1994; PHILPOTT et al. 2008) are needed. VANDERMEER et al. (1998) described a useful framework for the classification of the curves relating biodiversity loss to habitat management intensification, based on a four-type classification scheme (Fig. 1).

In this study, changes in ground-foraging ant assemblages along an agricultural intensification gradient were analysed in the Neotropic ecozone (Caribbean side of Nicaragua, Central America). Ants were chosen because of their proven responsiveness and robustness as bioindicators in a range of disturbed habitat contexts (FOLGARAIT 1998; AGOSTI et al. 2000; DUNN 2004), their relevance as a major component of tropical insect biomass (HÖLLDOBLER & WILSON 1990) and their important role in structuring faunal and floral communities (DAVIDSON et al. 1978; ANDERSEN 1992).

Five habitat types were compared: forest, shade coffee, cocoa and corn plantations, and an active pasture. The aim of this study was to describe how ant species'

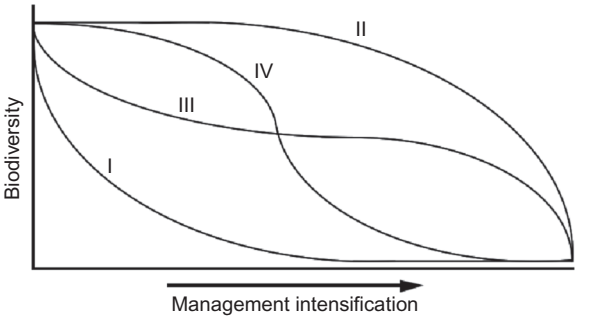

Fig. 1. — The four main patterns of biodiversity changes along an agricultural intensification gradient. Type I is the curve implicitly assumed by most pristine-habitat conservationists, where biodiversity dramatically declines as soon as any human use and management is brought to bear on the ecosystem. Other types are ranked in order of decreasing effect. Based on VANDERMEER et al. (1998).

richness and diversity change along the disturbance gradient represented by the five habitat types, following the framework provided by VANDERMEER et al. (1998).

METHODS

Study area

The study was carried out in the surroundings of Kubalí, near Waslala (13°20'N, 85°22'W), in the Región Autónoma del Atlantico Norte (RAAN), Nicaragua. The climate is tropical, with annual precipitation ranging between 1300 and 1500 mm. The rainforest, which originally covered the area, has been cleared and replaced by agricultural fields (mainly pastures, abandoned land and corn but also small coffee and cocoa plantations); the only significant exception being the nearby Bosawas Nature Reserve. The majority of farms have a size of about 20 ha or less and cultivations are arranged in small plots (about 3–5 ha). The scarce rainforest remnants (usually less than 10 ha each) are located on steep slopes of hills unsuitable for agriculture and are interspersed in a habitat matrix composed of pastures, low-intensity small cultivations and abandoned patches in different stages of regeneration.

Sampling design

Five habitat types were identified, corresponding to a gradient of management intensification:

(a) 'Forest', secondary forest fragments situated on the top of a hill (about 400 m altitude); this habitat represented the least disturbed ecosystem of the area. Maximum tree height was up to 25–30 m. The most common species were *Guazuma ulmifolia*, *Bursera simaruba* and *Calycophillum* sp., *Enterolobium cyclocarpum* and *Cordia* sp.
(b) 'Coffee plantation', represented by organic shaded plantations covered by remnants of the forest canopy and planted trees. No understorey was present except for the coffee bushes (height 1.5–2.5 m). These plantations broadly corresponded to the "traditional polyculture" in PERFECTO et al. (2005).
(c) 'Cocoa plantation', an organic shaded plantation with a dense, diverse multispecific covering of arboreal vegetation; the understorey was absent due to cultivation practices. The height of the cocoa plants was 2.5–5.5 m. The most common shade species were *Inga* sp., *Cordia alliodora*, but also *Mangifera indica*, *Persea americana* and *Citrus* spp. were present.

(d) 'Corn plantation', representing the most intensive cultivation in the study area. Trees and understorey were absent and the plantation was strictly monospecific. No chemicals were used and ploughing was rarely performed.
(e) 'Pasture', corresponding to the highest degree of disturbance in the area: no trees or bushes were present and cattle was let free to graze.

For each habitat type, two replicate areas of at least 3 ha were identified and four square plots (10 × 10 m) were established at random in each area. In each plot, tuna baits (ca 1 cm^3) were placed on the ground to form a 3 × 3 grid system with baits 5 m apart from each other. A total of 72 baits/habitat were placed (36 per replicate area). A distance of at least 25 m was left among grids to ensure independence of capture events (MAJER 1980). Furthermore, baits were placed at least 30 m from the edge of the habitat. Ants found on baits 45 min later were collected and preserved in alcohol for further identification. The order of bait placement was randomised and replicate grids were set up on different days within each habitat type and area. The study was carried out during March–April 2006.

Data analysis

Ants were identified to the species level when possible, following BOLTON (1994) and the "Ants of Costa Rica Identification Guide" provided by J.T. LONGINO (http://www.evergreen.edu/ants/AntsofCostaRica.html).

The resulting presence/absence matrix was used as input for subsequent analyses. The Jacknife-2 richness estimator (MAGURRAN 2004) was computed for each site and each habitat type separately using the EstimateS package (Ver. 7.50; COLWELL 2005). Richness estimates among the different habitat types were compared following SAUER & WILLIAMS (1989), using the Contrast software (HINES & SAUER 1989). Diversity was computed using the inverse Simpson index (MAGURRAN 2004).

Multivariate data analyses were performed using the occurrences of each species as input. The occurrences of a species in a grid were calculated as the number of baits where the species was recorded (value ranging between 0 and 9). The multivariate distances among samples were computed using the Bray–Curtis dissimilarity index and the resulting distance matrix was analysed by non-metric multidimensional scaling (NMDS) according to CLARKE & WARWICK (2001), using the Primer v5 package (Primer-E Ltd). Differences in species composition among habitat types were analysed by permutation-based non-parametric multivariate analysis of variance (npMANOVA), as described in ANDERSON (2001). Two factors were considered: 'habitat' (fixed factor with 5 levels) and 'area' (random factor nested in 'habitat', 2 levels). Multiple comparisons among each pair of habitat types were performed using Bonferroni corrected t-tests (QUINN & KEOUGH 2002).

RESULTS

Ant species richness

In total, 70 species belonging to 20 genera were collected (Appendix I). Twelve species were collected in the pastures (8 in the first and 10 in the second, respectively), 18 in the corn fields (17 and 13), 19 in the coffee plantations (14 and 12), 27 in the cocoa plantations (17 and 20) and 37 in the forest plots (24 and 25). Fig. 2 shows the Jacknife-2 accumulation curves of each habitat type (two replicate areas pooled). The estimator curves grew almost asymptotically, with the exception of the curve of the cocoa plantation, which presented a clear linear increasing trend. As expected, the forest site had the highest richness (estimated richness, ER = 57) while the pasture had

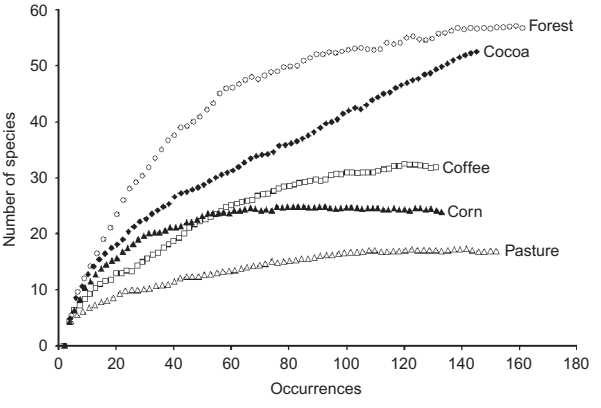

Fig. 2. — Jacknife richness estimator curves of the five habitats.

the lowest richness (ER = 17). Cocoa ranked second (ER = 53), followed by coffee (ER = 32) and corn (ER = 24). All the differences among habitat types were statistically significant ($P < 0.05$). Similarly, Simpson diversity was maximal in the forest plots (D = 9.047), followed by cocoa (D = 7.124), coffee (D = 4.700), corn (D = 4.349) and pasture (D = 4.394).

Assemblage composition

Summary values are reported in Table 1. The greatest number of unique species (i.e. species found only in one specific habitat type) was found in the forest, while the plots with the lowest number of unique species were in the coffee and corn plantations (4 each). In general, the pasture had between zero and a few species shared with the shaded plantations and the forest, and more with the corn fields. Forest plots, in contrast, had more species shared with the cocoa and coffee plantations than with the

Table 1.

Number of species, unique and shared species.

Habitat	Number of species	Unique species	Shared species			
			Forest	Cocoa	Coffee	Corn
Forest	37	19	—	—	—	—
Cocoa	27	9	12	—	—	—
Coffee	19	4	11	11	—	—
Corn	18	5	5	9	6	—
Pasture	12	6	0	3	2	6

Unique species were defined as the species found in only one habitat type, while shared species were defined as species observed in two different habitats.

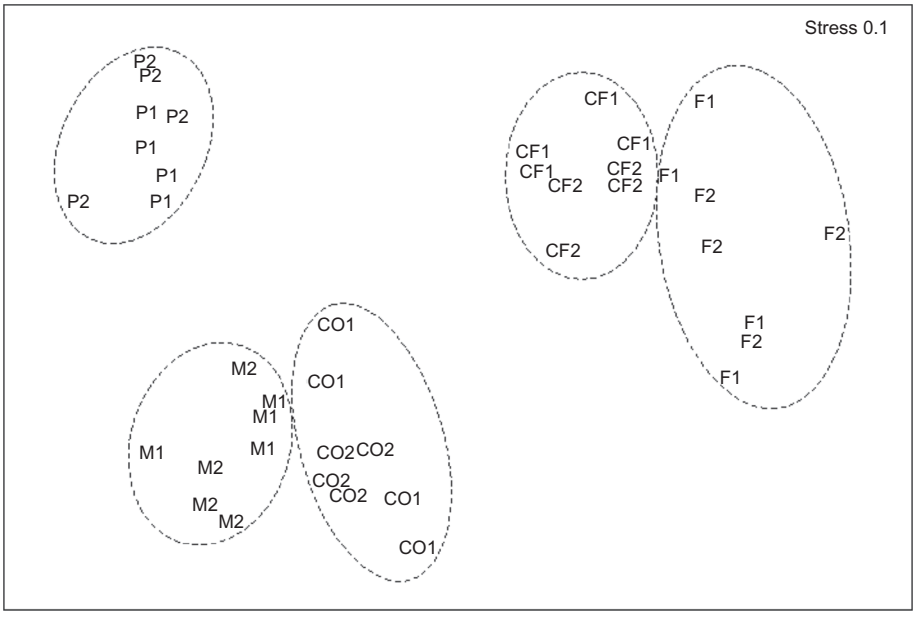

Fig. 3. — NMDS ordination plot. F = Forest, CF = coffee, CO = cocoa, M = corn, P = pasture. Numbers refer to the two sampling areas for each habitat. The five habitat data clouds are encircled for clarity.

corn plantation or pasture. Cocoa had a comparable number of species in common with forest, coffee and corn (12, 11 and 9, respectively), while coffee had more species in common with the forest and cocoa plantations than with either corn or pasture.

Fig. 3 shows the NMDS ordination plot. The stress level was low (stress = 0.1), indicating that the two-dimensional representation adequately depicted the compositional differences among assemblages. The sample points of each habitat type were tightly grouped, with a clear separation among habitats. Furthermore, within each habitat, no clear segregation among points belonging to the different plots was evident. The position of sample points in the NMDS space was consistent with a gradient of management intensification: the samples from the pasture and those from the forest were located at the two extremes of the plot, with the plantations in intermediate positions. As expected, the corn plantation assemblage was most similar to that of the pasture. However, in contrast to the ranking obtained from richness estimates, the coffee plantation assemblage was closer to that of the forest, while samples from the cocoa plots were nearer to those of the corn fields. The npMANOVA test showed no effect from the factor 'area' ($F_{4,30} = 1.05$; $P > 0.4$), meaning that no difference was detected in the ant assemblages of the two replicate areas within each habitat. In contrast, there was a significant effect of 'habitat' ($F_{4,5} = 18.28$; $P < 0.001$). Multiple comparisons revealed a significant difference between all the pairs of habitats (Bonferroni corrected t-tests, $P < 0.01$).

DISCUSSION

Species richness varied significantly among the different habitats, showing a decreasing trend from forest to pasture, passing through the different types of plantations.

The reduction in richness with respect to the forest was low in the cocoa plots (whose estimated richness was about 93% of that of the forest) and increased in coffee, corn and pasture. However, since the sampling in the cocoa plantation was probably not fully adequate, as suggested by the rising accumulation curve, all conclusions concerning this habitat must be considered with caution. In principle it is not impossible that more species could be found in the shaded plantations than in the secondary forest when this is represented by a small fragment, as in this study (Brühl et al. 2003; Vasconcelos et al. 2006).

Similar results were obtained for the assemblage compositions. The different plots were ordered in a clear sequence, with fairly well separated (and statistically significant) groups of observations. Indeed, the ordination plot broadly resembled the ranking of habitats obtained from richness estimates, albeit with some differences. The differences between the extremes of the series (forest-pasture) were clear and unambiguous, since these habitats shared no species (dissimilarity = 100%). As with the richness estimates, the corn plantation ranked second in terms of dissimilarity with the forest, with a low number of shared species (5 species). However, there was no full agreement between biodiversity and compositional patterns in the shaded plantations, with cocoa being more similar to the coffee plantations than to forest. This discrepancy with the richness ranking had different causes. First, although cocoa and coffee had comparable numbers of species in common with the forest plots (12 and 11, respectively), their relative importance was different. Species shared with the forest amounted to about 58% of all species observed in the coffee plantations versus 44% of total species richness in the cocoa plots; hence, the former was more similar to forest than the latter. Furthermore, these species generally had greater incidences in the coffee plots than in the cocoa ones. Secondly, 9 of the 27 species recorded in the cocoa plantation were only found in this habitat, while one species (*Azteca xanthochroa*) was unique to the coffee plantation. This suggests that, although poorer, the assemblage in the coffee was more similar to the forest. Finally, it must be remembered that, due to the not fully adequate sampling in the cocoa plots, any consideration about its associated ant assemblage should be considered with caution.

A question arises as to the origin of the observed differences between the coffee and cocoa assemblages, since it may have some relevance to conservation practices. Likely causes could involve a plethora of unknown local factors, including differences in the history of the plots or their neighbouring areas, or different management schemes. Indeed, many studies have shown ants' sensitivity to fine habitat features related to habitat maturity, land management and disturbance events (e.g. Majer 1983; Watt et al. 2002, just to mention a few), and we made no direct attempt to control for such effects. Moreover, within the same habitat type, management practices are known to considerably affect ant assemblages, and particular levels of shade may be important (Perfecto & Snelling 1995; Perfecto et al. 1997; Philpott et al. 2008) or specific shade trees may support higher diversity and abundances than others (e.g. Johnson 2000). There was a macroscopic difference between the vertical structure of the two types of habitats, at least in the study plots. In both types of plantations, the natural understorey was completely removed and the only significant plants under the tree canopy were either cocoa or coffee. The former, however, were small trees that were taller than the small coffee bushes. This difference in the vertical complexity of the two habitats may partly explain the differences in the associated ant assemblages, since it is known that vegetation structure can affect ant communities (e.g. Lassau & Hochuli 2004; Rios-Casanova et al. 2006; Vasconcelos & Vilhena 2006). However, this point requires further investigation.

Overall, the results from the coffee and cocoa plantations support the view that the biodiversity pattern in the managed systems is far from the pessimistic Type I (VANDERMEER et al. 1998) implicitly assumed as true by the 'pristine habitat conservationists' (Fig. 4). The observed decrease in richness reasonably falls between the Type III and Type IV curves, where biodiversity loss is reduced in the initial stages and falls off more considerably only when some critical management intensity is reached (see also SWIFT et al. 1979; PERFECTO et al. 2003). Yet, identifying the 'critical stage' is somewhat arbitrary and caution must be exercised, since the exact form of the curve heavily depends on the intensity measure used. Furthermore, our results suggest that the detection of a critical point may depend on the measure of diversity employed. Indeed, whereas univariate measures (species richness, diversity) placed the cocoa plantations very close to the forest and the coffee plantations close to the corn fields, multivariate analysis reversed this trend (but see the already discussed caveats about the adequacy of sampling in the cocoa plots).

Several caveats on the sampling design and procedures used are needed to interpret the results of this study. First, only ants foraging on the ground were sampled and this may in principle confound the differences between open and shaded habitats, given that in the latter arboreal species may represent a large component of ant fauna (although the *Crematogaster* and *Camponotus* species caught also in open habitats suggest that at least some of the arboreal species may come down the trunks of trees to forage on the ground and hence be captured). A second important issue is represented by the sampling method, which was based on tuna baiting. This technique has often been used as a reliable and fast sampling method for comparing ant assemblages in different habitat types (e.g. PERFECTO & VANDERMEER 2002; PERFECTO et al. 2003; PHILPOTT et al. 2008), and comparisons with different methods have yielded broadly consistent estimates (PHILPOTT et al. 2006). However, a fuller inventory of species could be

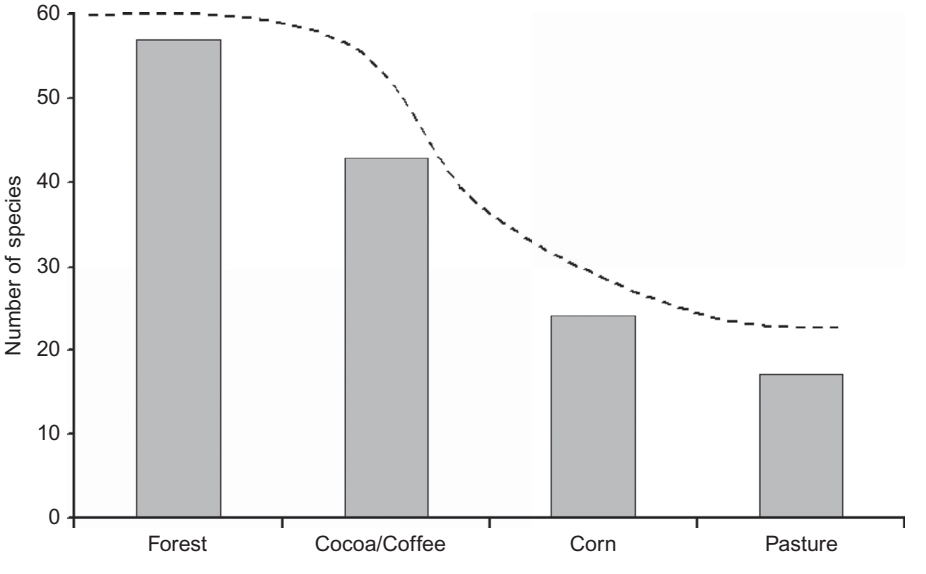

Fig. 4. — The observed richness pattern (bars) and the hypothetical model (dotted line). The 'Cocoa/Coffee' bar reports the average between the estimated richness of the two sites.

obtained by the simultaneous use of different sampling techniques (LONGINO et al. 2002, and references therein) and thus caution must be taken when interpreting the results. Secondly, sampling was limited in both space and time. Only two replicate areas were used for each habitat type and a greater sampling effort would provide a more reliable and general figure of the changes of ant assemblages associated with differences in management practices. The same point applies to the temporal aspects of sampling and a greater effort for temporal replication (different seasons, different times within each season) would be required. Finally, only ants foraging on the ground were sampled.

In conclusion, the results confirmed that traditional organic plantations may help to maintain high ant biodiversity levels, broadly comparable to those of the forest (see also REITSMA et al. 2001; PERFECTO et al. 2003; BANDEIRA et al. 2005; PINEDA et al. 2005; HARVEY et al. 2006; VAUGAN et al. 2007; BISSELEUA & VIDAL 2008, for other examples including other taxa). Such traditional land-use practices, when soundly calibrated and managed, may create new landscape elements and offer more scope for the conservation of biodiversity, at both the species and landscape levels.

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Appendix I.

Species captured in the five habitat types.

Species	Pasture	Corn	Coffee	Cocoa	Forest
Anochetus mayri					x
Apterostigma pilosum				x	x
Azteca xanthochroa			x		
Brachymyrmex heeri		x		x	
Camponotus novogranadiensis		x	x	x	
Camponotus planatus	x	x			
Camponotus sanctafidei					x
Camponotus striatus		x			
Cardiocondyla minutior	x				
Crematogaster curvispinosa	x				
Crematogaster longispina			x		x
Crematogaster nigropilosa			x	x	x
Crematogaster sumichrasti				x	
Crematogaster torosa				x	
Forelius pruinosus	x	x			
Gnamptogenys porcata					x
Gnamptogenys sp.				x	
Hypoponera nitidula					x
Hypoponera sp. (cf. *opacior)*					x
Hypoponera sp. (cf. *trigona)*					x
Mycocepurus smithii				x	
Nomamyrmex esenbeckii wilsoni				x	
Odontomachus meinati		x			
Pachycondyla apicalis					x
Pachycondyla harpax					x
Pachycondyla verenae		x			
Paratrechina caeciliae					x
Paratrechina guatemalensis	x				
Paratrechina steinheili		x		x	x
Pheidole acamata			x		x
Pheidole anastasii					x
Pheidole biconstricta			x		
Pheidole boruca				x	x
Pheidole browni					x

(*Continued*)

Appendix I.

(*Continued*)

Species	Pasture	Corn	Coffee	Cocoa	Forest
Pheidole celaena				x	
Pheidole dossena				x	x
Pheidole gulo			x		
Pheidole indagatrix		x	x	x	x
Pheidole laselva					x
Pheidole laticornis	x				
Pheidole nebulosa					x
Pheidole oaxana					x
Pheidole protensa			x	x	x
Pheidole pugnax	x	x	x	x	
Pheidole punctatissima			x		x
Pheidole radoszkowskii		x			
Pheidole rhinoceros					x
Pheidole rogeri			x		x
Pheidole sp. (cf. *bilimeki)*					x
Pheidole sp. (cf. *flavens)*			x	x	
Pheidole sp. (cf. *indistincta)*		x			x
Pheidole sp. (cf. *rugiceps)*				x	x
Pheidole sp. (cf. *simonsi)*			x	x	x
Pheidole sp. (cf. *susannae)*					x
Pheidole sp. (cf. *variegata)*		x			
Pheidole sp. (*fallax* group)					x
Pheidole sp. (*tristis* group)					x
Pheidole scalaris				x	
Pheidole subarmata	x	x		x	
Pheidole susannae		x	x	x	x
Procryptocerus pictipes				x	
Pseudomyrmex elongatus			x		
Pseudomyrmex gracilis	x	x			
Pseudomyrmex pallidus	x				
Pseudomyrmex tenuis				x	
Solenopsis castor					x
Solenopsis geminata	x	x	x	x	
Solenopsis hayemi	x				
Solenopsis picea		x	x	x	x
Wasmannia auropunctata			x	x	x